

OVER-EXPLOITATION OF LARVAL HOST PLANTS BY THE  
BUTTERFLIES *HELICONIUS CYDNO* AND *HELICONIUS SAPHO*  
(LEPIDOPTERA: NYMPHALIDAE: HELICONIINAE:  
HELICONIINI) IN COSTA RICA?

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*Abstract.*—I examined two small individuals of a larval host plant species (*Granadilla* sp.) of *Heliconius cydno* and *H. sapho* (Lepidoptera: Nymphalidae: Heliconiinae: Heliconiini) in northeastern Costa Rica to determine approximately the degree to which each one was utilized repeatedly. From the rather detailed conceptual framework and ecological studies of *Heliconius* butterflies I expected to find low clutch size and exploitation of fresh meristem for *H. cydno* and *H. sapho* as members of the “*Granadilla*-feeding” species group. The observations on one of the two plants agreed well with these expectations. On the other host plant individual, however, females of these species placed unusually high numbers of eggs on available fresh meristem. In subsequent observations when no apical meristem was present, no immature stages were found. The subtle interplay of many environmental factors, including shifting scarcities of fresh meristem on host plants, determines the intensity of oviposition on a particular plant.

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### Introduction

In some butterflies females searching for oviposition sites do not always accurately assess the suitability of a host plant individual in terms of larval growth and survival (Chew 1977). The pattern of egg placement on individual host plants by species which oviposit singly is often determined by the degree of patchiness of the host plant species (Chew 1977; Benson 1978; Young 1980). In many tropical butterflies such as *Parides*, females often place eggs on tiny seedlings of the host plant, clearly too small to support larval growth (Young, pers. obs., 1969-80, Costa Rica). But in some groups such as the Heliconiinae exploiting the Passifloraceae as larval host plants (Brower and Brower 1964; Gilbert 1975; Benson et al. 1976, and several other references) there appears to be careful assessment of host plant individuals by female *Heliconius* (Benson et al. 1976; Benson 1978). It is therefore of considerable interest to report here patterns of repeated exploitations of individuals of a host plant of *Heliconius cydno* in Costa Rica. An incidence in which a related species, *Heliconius sapho*, overexploited one of the host plants used by *H. cydno* is also reported.

### Materials and Methods

I observed female *H. cydno* deposit eggs on two immature individuals of *Granadilla* in northeastern Costa Rica. I also discovered a large number of eggs of *H. sapho* on one of these plants. The general locality is a 4,000-acre farm complex about 8 km north of La Virgen, Heredia Province, a region within the premontane tropical wet forest zone (220 m elev.) (Holdridge 1967). Information on the biology of *H. cydno* and *H. sapho* in Costa Rica has been summarized elsewhere (Smiley 1978; Young 1973, 1978). Both species are abundant along borders of forest.

The initial observations of *H. cydno* at one host plant were made on February 14, 1977. I marked the location of the plant, took notes on its size and appearance (number of fresh and old leaves, herbivore damage, etc.), and returned many times until March 6, 1977 to make observations on the eggs and larvae present. I examined the patterns of larval feeding and any interactions among larvae.

The specific locality of the first plant is "Finca La Tigra," mixed cacao (*Theobroma cacao* L.) plantations and various stages of forest succession. On August 3, 1978 I discovered *H. cydno* ovipositing on another individual of the same plant species but this time at "Finca El Uno," an area of cacao, *Hevea* rubber, and strips of young secondary succession about 5 km from the "La Tigra" site. I recorded the immature stages present and made observations until August 8. The location of this plant was marked and I returned to examine for the presence of *H. cydno* or other *Heliconius* in five additional periods: December 1-4, 1978; March 12-20, 1979; June 30, 1979; September 11, 1979; and February 21-22, 1980. Each time I recorded the appearance of the plant, noting presence of fresh leaves and other features. Upon returning to the site of the "El Uno" plant on June 13, 1980 I noted the presence of new meristem and many eggs scattered on it. Observations were made through July 2 during which it was determined that the species was *H. sapho*. I observed the abundance of larvae and their distribution on the plant.

### Results

The host plant is an immature *Granadilla*, a subgenus in the passifloraceous subfamily Laurifoliae, which consists chiefly of small, erect plants without tendrils (Dr. K. S. Brown, Jr., pers. comm.). The plant is possibly *Passiflora guazumaefolia*. At this locality *H. cydno* oviposits on at least one other *Passiflora*, this time a vine, *P. vitifolia* with different taxonomic affinities within the family (Young 1978). Owing to the tentative nature of host plant identifications I refer to them as "Granadilla A" (La Tigra) and "Granadilla B" (El Uno).

"Granadilla A".—This individual was found in a light gap along a well-

shaded footpath (Fig. 1A) in disturbed primary forest and at the time of its discovery it had four fresh leaves (new meristem) (Fig. 1B). The plant was about 0.25 m tall (Fig. 2A) with few signs of herbivore attack to both older leaves or fresh meristem. At 1130 hours on February 14, 1977 one "fresh" female *H. cydno* was noticed inspecting the plant and two eggs were placed on it within a 20-minute period. The first egg was deposited at 1140 hours next to the midrib on the ventral side of one of the apical fresh leaves; a second egg was already present on the same leaf. Another egg was placed on the petiole of a fresh leaf (Fig. 2B) ten minutes later. No additional eggs were found. Judging from the white color of the egg already present, this egg was probably a few days old and possibly not from the same female witnessed placing two eggs. Fresh eggs of *H. cydno* are yellow (Young 1973). This plant had a total of ten leaves, including the fresh ones. No other *Heliconius* eggs or larvae were found on the plant.

The following day the older egg hatched and matched the general description for the first instar of *H. cydno* (Young 1973). This larva rested on the tip of the fresh leaf bearing the two eggs. Later that day one of the other eggs disappeared, possibly the result of predation by ants or cannibalism by the larva present. At 1530 hours that day, an ant approached the larva and it dropped on a silken thread from the leaf. Several small reddish-brown (unidentified) ants were seen at the conspicuous extra-floral nectaries on the petiole of one of the lower yet fresh leaves. On the following day (February 16) the larva had eaten away a strip of fresh leaf tissue on the leaf bearing the surviving egg. Later that day a new egg was found on the petiole of another fresh leaf.

The first instar begins feeding from the edge of a fresh leaf, cutting deep notches into the tissue and eventually reaching the midrib area. This larva stayed on the same fresh leaf for all five instars, completing molt cycles on it and eventually developing a feeding pattern in which entire sections of the leaf are chewed away (Fig. 3A, B). Prior to pupating it eventually moved onto two other fresh leaves at the top of the plant and attaining a body length of about 35 mm. The two additional eggs present disappeared and this larva was the only one on this plant for the study period.

I noticed that the larva fed both day and night, but intermittently and with no consistent pattern. The larva eventually pupated on an older leaf of the host plant. It is estimated that the larvae ingested approximately 140 mm<sup>2</sup> of fresh leaf tissue by the time of pupation. Older leaves were not consumed. The portion of fresh leaf tissue consumed represents about 60% of the total amount of fresh leaf tissue available on the plant during the study period. No additional fresh leaves were produced during this period. Other than the total of four eggs counted in the first few days, no additional eggs were found thereafter.

"*Granadilla B*".—This plant was discovered again as the result of an *H.*





Fig. 1. (A) The forest habitat understory where "*Granadilla A*" was discovered. (B) "*Granadilla A*" showing the fresh meristem (stem and leaves) contrasting in shade from older leaves.

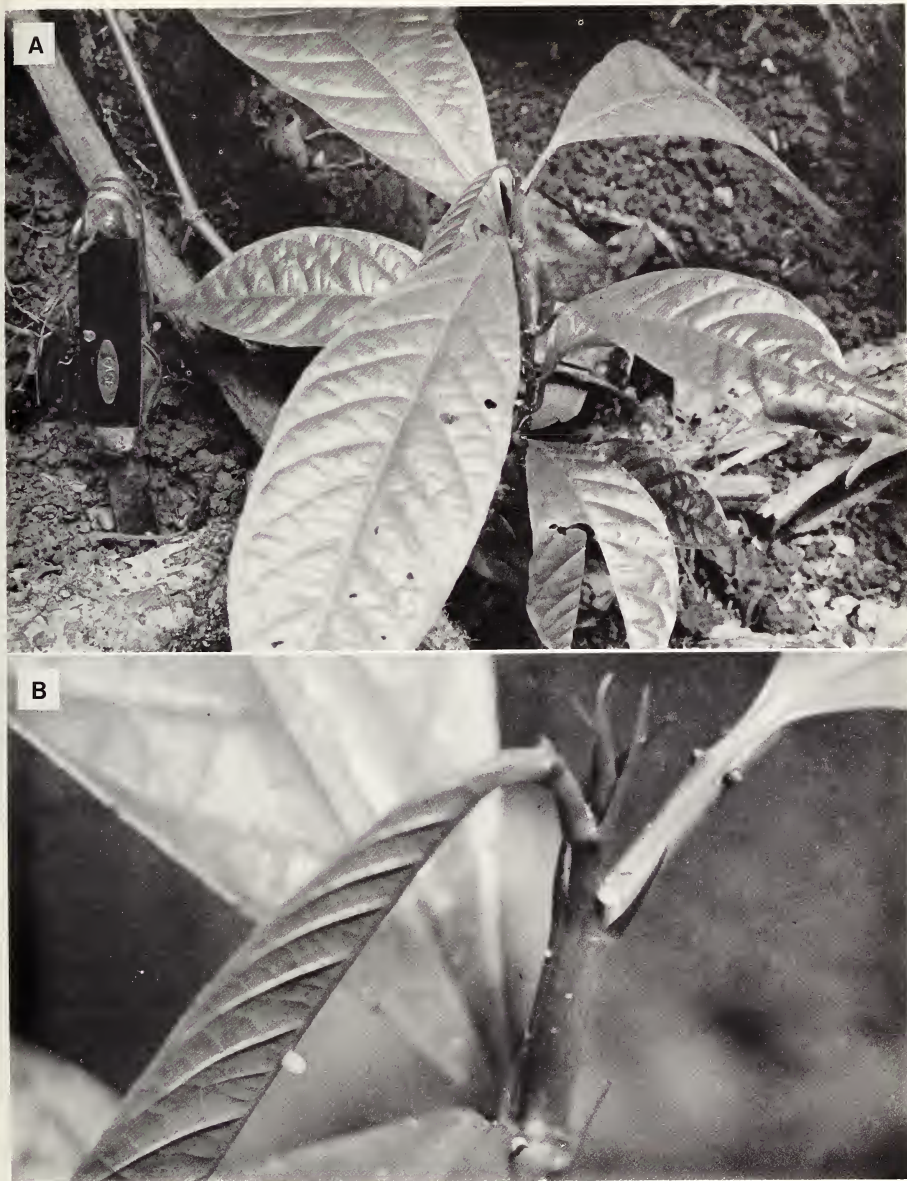


Fig. 2. (A) The fresh leaves and other parts of meristem on "Granadilla A"; note few signs of any appreciable herbivore damage. (B) Positions of two eggs of *Heliconius cydno* on the fresh meristem of "Granadilla A"; note that one egg is near the midrib of a young leaf while the second egg is at the base of the petiole; note the conspicuous extrafloral nectaries on a petiole to the right.



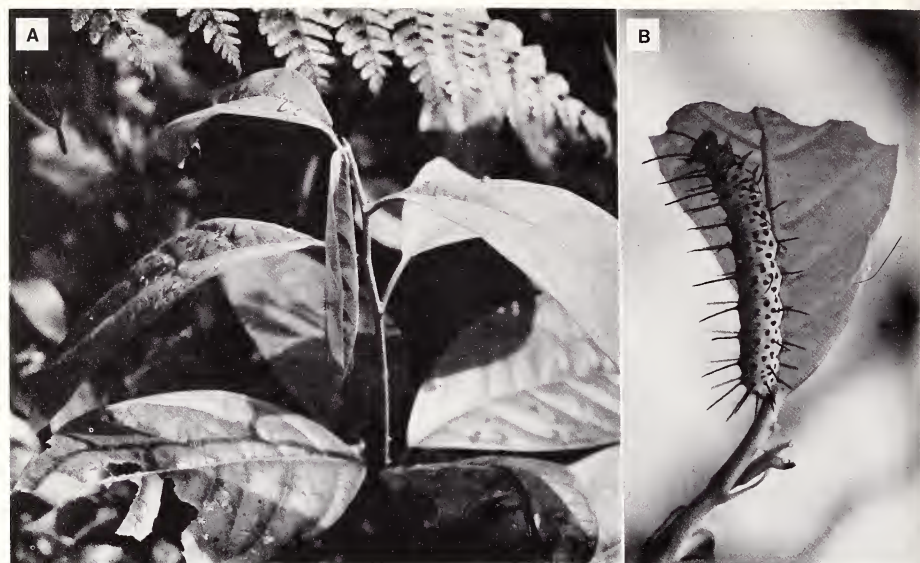


Fig. 3. (A) Note the damage from feeding by the larva of *H. cydno* on the fresh leaf in the lower left. (B) Fourth instar larvae of *H. cydno* with typical pattern of damage to a fresh leaf on "Granadilla A".

*cydno* female inspecting it (August 3, 1978, 0930 hours). It was found in a strip of dense herbaceous vegetation along a shaded trail within a cacao plantation. The plant was about 0.30 m tall when discovered and of a total of 12 leaves present six were fresh meristem. As with the first plant, the fresh leaves are easily distinguished from the older ones by their light green color and soft texture. The plant was actually a sucker shooting up from a thick woody stem.

A tattered female of *H. cydno* deposited a total of 15 yellow eggs on the apical stem of this plant (Fig. 4A) within a ten-minute period on the morning of discovery. The butterfly made four different visits to the plant, after flying off and fluttering through nearby vegetation before returning to deposit more eggs. The eggs were placed singly (Fig. 4B). Within five days after oviposition the folded apical region of the host plant had "leafed out" (Fig. 4C), making a spectacular display of bright yellow eggs packed into a relatively small area of fresh leaflets and stem. The result is a "loose" clustering of many eggs on the apical and fresh portion of the plant (Fig. 4C). An examination of the plant following the oviposition revealed no additional eggs or larvae, although an empty pupal shell of *Heliconius* was found on a seedling adjacent to the host plant. At the time of oviposition a raiding column of army ants (*Eciton* sp.) passed within a few centimeters of the host plant but did not affect oviposition.



Fig. 4. (A) *Heliconius cydno* in the act of placing several eggs on the fresh meristem of "Granadilla B". (B) Egg of *H. cydno* on the fresh petiole of "Granadilla B". (C) The distribution of 15 eggs of *H. cydno* on the unfolded fresh leaflets and stem of "Granadilla B".

Egg number remained the same for the first four days following the burst of oviposition activity. By the fifth day, however, there were only eleven eggs and no first instar larvae to account for the remaining four. One of the remaining eggs was shriveled up. The same plant was re-examined in December and two larvae (second instar and third instars) of *H. cydno* were present on the plant (December 1, 1978). No eggs were present. At this time the plant was about 30 cm tall with roughly 50% of the biomass being fresh. The two larvae occupied different leaves. Several ants were seen patrolling the apical area of the plant on two days following the discovery. For the period March 12–20, 1979 fresh leaves were entirely absent from the plant and no *Heliconius* early stages were found. The plant was about the same size as it was in the previous December although no new growth was present. I noticed three fresh adults of *Philaethria dido* (Heliconiinae) flying in

the vicinity of the plant on one day. The general condition of the herbaceous vegetation was lush at this time. The plant was in the same general condition on June 30, 1979 and no early stages of *H. cydno* were found on it. The plant was briefly observed in September 1979 and February 1980 and again there was no new growth and no signs of *H. cydno* on it.

The plant was re-examined on June 13, 1980 at which time it had fresh meristem about 40 cm high and bearing eight full-sized and folded leaflets. The bottom woody part of the plant had ten old leaves. A total of 20 *Heliconius* egg shells were found scattered on the fresh leaflets and there were 14 second instar larvae in a tight aggregation on one leaflet. No unhatched eggs were present. By June 16 only eight larvae remained and the leaflets were now completely unfolded and the egg shells gone. No observations were made until June 29 at which time it was discovered that all of the fresh meristem had disappeared and that only one chrysalis was present on an older leaf. A thorough search of the surrounding vegetation within a four-meter square area failed to turn up additional chrysalids. The chrysalis hatched July 2 and proved to be *H. sapho*.

### Discussion

*Heliconius cydno* and *H. sapho* are species in the "melpomene" group, being closely allied with other species such as *H. pachinus*, *melpomene*, and *heurippa* (Brown and Mielke 1972; Benson 1978). The species are classified as laying medium to large eggs, solitary meristem feeders as a larvae, and generally requiring large host plant individuals (Benson 1978). The clutch size is generally small (Benson 1978) and a species such as *H. melpomene* places eggs singly on subterminal leaflets and young tendrils (Alexander 1961). The usage of meristem tissues by *Heliconius* species comprises a major aspect of the radiation of the group (Benson et al. 1976). *Heliconius cydno* is oligophagous while the allied *H. melpomene* in Costa Rica is monophagous (Smiley 1978). The species oviposits on at least one non-*Granadilla* host plant at the site of the present study (Young 1978) as it does in a Costa Rican mountain wet forest site (Young 1973). *Passiflora vitifolia* is a common and widespread host plant of *H. cydno* and several other *Heliconiinae* at the study site (Young 1978) as well as at nearby "Finca La Selva" (Smiley 1978). Twenty-seven species of *Granadilla* are used by at least eight species in the "transitional" and *melpomene* groups (Benson et al. 1976).

Many species in the "Granadilla-feeding" group (Smiley 1978) place eggs singly on fresh meristem and the larvae feed primarily on these tissues (Benson et al. 1976). The availability of fresh meristem is a limiting factor in the populations of some *Heliconius* species (Benson 1978; Smiley 1978). The butterflies are adapted for searching for and placing eggs on this portion of the individual host plant (Gilbert 1975).



Assuming that the observed host plant was indeed *P. guazumaefolia* and the fact that many species in the *Granadilla*-lineage of the Passifloraceae have conspicuous extrafloral nectaries that attract ants (Gilbert 1975; Benson et al. 1976) the observed loss of eggs, apparently from ant predation, is not unexpected. It is also known that some species of *Granadilla* possess stipules resembling *Heliconius* eggs and larvae (Benson et al. 1976) thus discouraging repeated oviposition in *Heliconius* which place eggs singly on meristem. Such factors reduce the likelihood that a female *Heliconius* will oviposit repeatedly on the meristem of a particular individual of the host plant species available in the habitat. The species of *Heliconius* exploiting such host plants generally have aggressive larvae so that there is usually no more than one larva per meristem (Benson et al. 1976).

Yet "*Granadilla B*" presents a different picture. The observed placement of fifteen eggs on a single fresh meristem by *H. cydno* is a notable departure from the expected clutch size. The usual clutch size of this species is small (1-3 eggs per plant) (Benson 1978; Young 1978). Presumably the plant was too small to support all of the larvae. Perhaps ant predation and aggressive interactions among the larvae would have taken a heavy toll thus reducing effective clutch size considerably. The apparent placement of 20 eggs on fresh meristem of the same plant by *H. sapho* and the subsequent dwindling of larvae in this gregarious species is a further indication of the interaction of reduced food supply and possibly predation as reducing larval numbers in this species. Presumably the eggs were placed in a relatively loose cluster at an even earlier stage in the unfolding of the fresh meristem. The data suggest that the larvae defoliated the plant of the fresh meristem and that only a portion of them survived.

Why should some *Heliconius* "invest" about five times the expected number of eggs in a small individual of *Granadilla*? The answer is clearly beyond the scope of this paper, yet it is interesting to suggest one explanation based upon the concept of limiting resources affecting the butterfly at the study site. The consecutive choices by a female butterfly searching for oviposition sites is influenced greatly by the spatial distribution of suitably host plant individuals (Chew 1977; Benson 1978; Young 1980). If host plant individuals are very patchy and concealed, one might expect exploitation of alternative host plant species or more intense exploitation of the individual host plant when encountered. Although several species of host plant might be available in the habitat, their suitability for oviposition by meristem specialists such as *H. cydno* and *H. sapho* is determined largely by the availability of fresh meristem tissues. My general impression of the relative abundance of *P. vitifolia* to *P. guazumaefolia* at the locality of the present study is that the former species is far more abundant. There seems to be a greater number of patches per unit of habitat and the biomass of each patch is considerably larger. Whether or not *H. cydno* and *H. sapho* exhibit a physiological preference for one species over the other is not

known, although one study showed that the *H. cydno* exhibits approximately equal oviposition frequency on several host plant species in different subgenera (Smiley 1978). Therefore the differential in terms of actual host plant usage in the wild is probably largely determined by relative patch structures among host plant species and the availability of fresh meristem among the species.

The scarcity of *Granadilla* (*P. guazumaefolia*) coupled with perhaps reduced availability of fresh meristems on other host plants such as *P. vitifolia* may induce repeated oviposition on small patches of those host plants with fresh meristem. Chew (1977) noted that there is sometimes considerable discrepancy between oviposition behavior and the suitability of the chosen host plant individual for larval growth. I have noted similar situations in *Parides* (Papilionidae) ovipositing on *Aristolochia* seedlings and *Morpho peleides* oviposit on tiny seedlings of *Machaerium seemanii* in Costa Rica.

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#### Literature Cited

- Alexander, A. J. 1961. A study of the biology and behavior of the caterpillars, pupae, and emerging butterflies of the subfamily Heliconiinae in Trinidad, West Indies. I. Some aspects of larval behavior. *Zoologica* 46:1-24.
- Benson, W. W. 1978. Resource partitioning in passion vine butterflies. *Evolution* 32:493-518.
- , K. S. Brown, Jr. and L. E. Gilbert. 1976. Coevolution of plants and herbivores: Passion flower butterflies. *Evolution* 29:659-680.
- Brower, L. P. and J. V. Z. Brower. 1964. Birds, butterflies, and plant poisons: A study in ecological chemistry. *Zoologica* 49:137-159.
- Brown, K. S., Jr. and O. H. H. Mielke. 1972. The heliconians of Brazil (Lepidoptera: Nymphalidae). Part II. Introduction and general comments, with a supplementary revision of the tribe. *Zoologica* 47:1-40.
- Chew, F. S. 1977. Coevolution of pierid butterflies and their cruciferous foodplants. II. The distribution of eggs on potential foodplants. *Evolution* 31:568-579.
- Gilbert, L. E. 1975. Ecological consequences of a coevolved mutualism between butterflies and plants, p. 210-240. *In*: L. E. Gilbert and P. H. Raven, eds., *Coevolution of Animals and Plants*. University of Texas Press, Austin. 246 p.
- Holdridge, L. R. 1967. *Life Zone Ecology*. Tropical Science Center, San Jose, Costa Rica. 104 p.
- Smiley, J. 1978. Plant chemistry and the evolution of host specificity: new evidence from *Heliconius* and *Passiflora*. *Science* 201:745-747.
- Young, A. M. 1973. Notes on the biology of the butterfly *Heliconius cydno* (Lepidoptera: Heliconiinae) in Costa Rica. *Wasmann J. Biol.* 31:337-350.

- . 1978. "Disappearances" of eggs and larvae of *Heliconius* butterflies (Nymphalidae: Heliconiinae) in northeastern Costa Rica. *Entomol. News* 89:81-87.
- . 1980. Evolutionary responses by butterflies to patchy spatial distributions of resources in tropical environments. *Acta Biotheoretica* 29:37-64.

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